

XXI. *Mimetic North American species of the Genus Limenitis (s.l.) and their models.* By EDWARD B. POULTON, D.Sc., M.A., LL.D. (Princeton), F.R.S., etc., Hope Professor of Zoology in the University of Oxford, Fellow of Jesus College, Oxford.

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## INTRODUCTION.

THE mimetic species of the North American Nymphaline genus *Limenitis* (including *Basilarchia*) superficially resemble, in the east and north, as suggested by Doubleday (Gen. Diurn. Lep., ii, p. 275), models belonging to (1) the *Danainæ* and (2) the *Papilioninæ*: in the west (3) a Nymphaline model generally placed in the South American genus *Adelpha*, allied to *Limenitis*.

A species of *Limenitis*, in many respects relatively ancestral and probably resembling the form from which the mimics arose, still exists in the east, and another in the west. Hence the history of the transformation—probably in every case very recent—can be made out with exceptional clearness.

The subject will be treated in the order in which the models have been arranged above.

I desire to thank Dr. F. Du Cane Godman, F.R.S., for

kindly lending me the specimens represented in Figures 2 to 8 on Plate XXV, and the authorities of the British Museum of Natural History for the originals of Figures 1 and 10.

#### THE DANAINÉ INVASION OF THE NEW WORLD AND THE CONSEQUENT MODIFICATION OF NORTH AMERICAN SPECIES OF LIMENITIS.

One of the most interesting problems of mimicry and migration in butterflies is raised by the consideration of these North American Danainés. The genera to which they belong extend throughout the tropical New World, but, although represented by excessively abundant individuals, they enter into no synaposematic relations with any of the Neotropical combinations. They mimic nothing and nothing mimics them in tropical America. On the other hand, in North America they supply models for some of the very best examples of mimicry in the North temperate zone. Considering these facts, it is clear that a suggestion published by the present writer in 1901 is erroneous. *Anosia plexippus* (*archippus*, F.) cannot have had its ancestral home in South America or have invaded the northern belt from the immediate south. The argument founded on a supposed southern source is, however, unaffected and has so direct a bearing on a common hypothesis as to the origin of mimetic resemblances that I venture to quote it on the present occasion:—"In the New World the genus *Limenitis* is confined to the Nearctic Region with the exception of a single species, a form of the mimetic *L. astyanax* (Fabr.), which just enters the borders of Mexico. If butterfly colours and patterns are the expression of the direct influences of the environment, then it is clear that the indigenous non-mimetic species of *Limenitis* (*Basilarchia*) are an expression of Nearctic conditions, and according to the theory of External Causes, the invader from the South should have come to resemble them instead of drawing an ancient Nearctic species far away from the ancestral colours and patterns into a close superficial likeness to itself."\* This argument is, as I have said, unaffected, because the Danainé is clearly an invader, although not from South America.

\* "Verhandl. d. V. Internat. Zool. Congr. z. Berlin." Jena, 1902, p. 171.

The argument may be briefly recapitulated as follows:—

The fact that the distasteful foreign species, invading temperate North America from a very different area, should not only maintain their characteristic original appearance under such different conditions, but should compel the ancestral residents in their new home to resemble them, is entirely inconsistent with an interpretation of mimicry based upon the supposed influences of locality (soil, food, climate, etc.).

In attempting to make out the past history of the North American Danaines, it is of paramount importance to ascertain their affinity with the Old World species; for it is admitted that their relationship to all other New World genera is remote. Rothschild and Jordan have recently stated that *Tasitia* is inseparable from the genus *Danaida* (*Limnas*) which contains the well-known *chrysippus*, L., and its forms.\* I therefore wrote to my friend Dr. Karl Jordan, enquiring whether he had considered the affinity of these forms to the New World *Anosia* and the Old World *Salatura*. He kindly replied as follows:—"I think that all the tawny Danaids [*Limnas*, *Salatura*, *Tasitia*, *Anosia*] are one genus, with the exception of the large [*Anosia*] *plexippus*. This insect differs as larva in having only two pairs of filaments† and as imago in the cell of the hind-wing being very long. The differences given by Moore for *Limnas*, *Tasitia* and *Salatura* do not at all hold good, neither the shape of the wings nor the position of the veins being constant."

Accepting this conclusion, the name *Anosia plexippus*, L. (*archippus*, F.), will be retained in the present memoir, while *berenice*, Cr., and its form *strigosa*, Bates, will be placed in the genus *Danaida*. It is impossible to speak with certainty as to the Old World species which most nearly represent the invading ancestors of the North American Danaines. A safe conclusion can only be arrived at after a searching investigation into the structural details of many species. But there can be little doubt that *Danaida* (*Salatura*) *genutia*, Cr. (*plexippus*, L.), presents many of the features of this ancestor. Thus the white markings upon the hind-wing under surface of *D. berenice*

\* "*Danaida chrysippus* cannot be generically separated from the American *gilippus* and *berenice*, *Limnas* being a synonym pure and simple of *Tasitia*." Nov. Zool., vol. x, Dec. 1903, p. 502.

† See, however, the note on p. 488.



are practically identical with those of *genutia*. The distribution of the latter also favours the same conclusion, for it extends far beyond the tropics into Western and Central China.

*Anosia* is the outcome of a much earlier invasion, allowing time for modification and the acquisition of characters of generic rank in the new home. *Danaida berenice* is the result of a far more recent immigration. The Old World parents of the two American forms were probably closely allied or may even have belonged to the same species at different periods of its history. There is strong evidence in the mimicry of these two genera by species of *Limenitis* (*Basilarchia*) that the relative periods of residence in North America were as they have been indicated above. Details will be supplied in later pages. It will be sufficient to point out here that the evolution of *L. archippus*, Cr. (*missippus*, F.), from the characteristic type of Holarctic *Limenitis* presented by its ancestor *L. (B.) arthemis*, Drury, has involved an entire change to a new and highly elaborate pattern on both surfaces,—a process which even the most ardent mutationist can hardly conceive to have been a rapid one,—especially when the mimetic pattern hits off so precisely the characteristic details of the model. *Danaida berenice* has however merely modified into resemblance with itself—a likeness attained by a few simple but perfectly effective changes—the mimic already fully formed under the influence of *Anosia*. In fact, distinct and evident details of the earlier mimicry of *L. (B.) archippus* still persist, and somewhat detract from the mimetic resemblance attained by its descendant, *floridensis*, Streck. (*eros*, Edwards).

The effects produced by both Danaine models upon the butterfly fauna of North America, combined with the absence of such effects in the tropical New World, support the conclusion that residence in the north has been far longer than in the south, and that the south was reached by way of the north. It is probable that the Old World ancestor of *Anosia* spread northward along the eastern borders of Asia, and entered America by way of the Aleutian Islands, and that its astonishing northern range dates back to the period of the invasion. The ancestor of *Danaida berenice* may have followed the same route during some temporary amelioration of climate, enabling this more tropical form to reach its present home in the New

World. At the northern boundary of the Neotropical Region—now running east and west from Mexico City to points on the Atlantic and Pacific coasts considerably further north—the southward migration of both *Danainæ* was probably checked for a considerable period. Held back for a time at the limits of that crowded area, teeming with the species of the allied *Ithomiinæ*, they finally in comparatively recent times forced their way southward and spread through South America, even reaching, in the case of *Anosia*, the south temperate zone. All this has been so recent that only insignificant changes—probably sub-specific—have occurred, and no mimetic or synaposematic relationship has been formed.\*

The hypothesis set forth above has the one merit that it accounts for the facts, puzzling as many of them are. The phenomena in the northern zone are unique, and as for those of the tropics, there is no other case where *Danainæ* of such marked size and appearance range through a crowded area without producing any effect on any member of the Lepidopterous fauna, or without themselves being affected thereby. If a striking comparison be desired, no better instance can be selected than the three African species of the genus *Melinda* (*Tirumala*), the products of an invasion from the Oriental Region. Of these three species *T. formosa*, Godm., and *T. mercedonia*, Karsch, are mimicked respectively by *Papilio rex*, Oberth., and its form *mimeticus*, Rothsch., while *T. morgeni*, Honrath, is itself mimetic of the characteristic Ethiopian Danaine genus *Amauris*.

It is, perhaps, unnecessary to state that in speaking of this Danaine invasion of tropical America, I leave out of account the remarkable *Danainæ* forming the section *Lycoræini*. These are at once shown by their structural peculiarities no less than by their intimate association with the great synaposematic groups to be very ancient inhabitants of the Neotropical Region.

#### THE EVOLUTION OF LIMENITIS (BASILARCHIA) ARCHIPPUS, Cr. (MISIPPUS, F.), AND ITS FORMS AS MIMICS OF THE INVADING DANAINES.

*L. archippus* is rightly considered by S. H. Scudder as the most striking example of mimicry in temperate North

\* It is however possible that a large Peruvian form of *Actinote thalia*, L. (or *anteas*, Dbl., Hew., if these two forms can be kept distinct), is an incipient mimic of *Anosia*.

America (" Butterflies of the Eastern United States and Canada," Cambridge, Mass., 1889, p. 718). It is, indeed, one of the most striking in the world. Before describing the evolution of its pattern from that of the ancestral *L. arthemis* it will be convenient to compare the distribution, habits, etc., of the two species.

*Limenitis archippus*, Cr.—Scudder states that this species ranges nearly all over the United States as far west as the Sierra Nevada, and, in Oregon and British Colombia, to the Pacific. It is however rare in the west, and unknown in Colorado, Arizona and New Mexico. It extends from Hudson Bay in the north to the Gulf of Mexico in the south. It is thus "found over very nearly the same area as *Anosia*" (l. c., p. 278).

Scudder describes its flight as "rather leisurely and sailing" (l. c., p. 277). It frequents "open country in fields and meadows, especially in low ground." Comparing its relative numbers with those of its parent *arthemis* and the sister species *astyanax*, Scudder states that *archippus* is "almost universally more numerous in individuals than the others" (l. c., p. 266). *Archippus* always appears to have two broods where the other two species usually have one.

The food-plants of the larva are willow and poplar, although many other plants are also recorded.

*Limenitis arthemis*, Drury.—Scudder speaks of this as a Canadian species *par excellence*, ranging over the whole width of Canada east of the Rockies, and far north to an unknown distance. It is also abundant in the northeastern States.

Scudder describes its sailing flight (p. 304), also stating that "it is very active, and has a rather short and rapid flight" (p. 303).

The earlier stages of the two eastern and northern mimetic species of *Limenitis* and their non-mimetic ancestor are, according to Scudder, only distinguished with difficulty (p. 254). *Arthemis* and *astyanax*, F., are, however, as we should expect, even more closely similar than *arthemis* and *archippus* (p. 255). The larva of *arthemis* feeds on a great variety of plants, including willow and hawthorn.

THE EVIDENCE THAT *LIMENITIS ARCHIPPUS* OCCURS AT THE SAME TIME AND PLACE AS ITS MODEL.\*

The following evidence (p. 455) bearing on the time and space relationships of *Limenitis archippus* and its Danaïne model exists in the bionomic series of the Hope Department. The most perfect data were those obtained on August 5, 1897, when, with my kind friends Professor W. M. Wheeler (now of Harvard) and Professor S. Watasé, I had an excellent opportunity of witnessing the flight of many examples of both model and mimic on the same ground.

One of the specimens, a female, captured on August 6, 1897, had evidently been visiting the flowers of the food-plant of its model; for abundant *Asclepiad* pollen-masses are attached to its limbs.

THE EVOLUTION OF THE MIMETIC PATTERN OF *L. ARCHIPPUS* FROM THAT OF THE NON-MIMETIC *L. ARTHEMIS*.

In the following interesting passage Scudder discusses the general principles by which, as we may believe, this remarkable transformation was effected:—

“It is to be presumed that the actual colors found in a mimicking butterfly are, with rare exceptions, such as existed somewhere in the ancestral form. In the case of our own mimicking *Basilarchia*, for example, whose orange ground tint is so totally at variance with the general color of the other normal members of the group, it will be observed that all the normal species possess some orange. Without this as a precedent fact, such perfect mimicry might perhaps never have arisen. Individuals among the normal species vary somewhat in this particular, so that

\* Much time and effort have been expended, during many years, in the Hope Department, to induce naturalists in the field to collect evidence bearing on the coincidence in time and space and on the habits of mimetic species and their models, to breed the seasonal forms of butterflies and accurately to record the times of their appearance in nature. Many of the results of this special study have been published. So far as I am aware, systematic attempts of the kind have been made by no other institution. I am bound to assume that the editor of “*The Entomologist's Record*” is ignorant of facts well known to probably every other student of insects in this country. However this may be, any reader of that publication can judge for himself how far the statements and inferences on pp. 189, 190 of the July number are true or false.—E. B. P., July 27, 1908.

MODEL. <i>Anosia</i> <i>plexippus</i> .	MIMIC. <i>Limenitis</i> <i>archippus</i> .	LOCALITY.	CAPTOR AND DATE.
1	2 (with 2 <i>L. arthemis</i> )	W. Manitoba, Russell, July 6, 1897, about 1600 ft.	H. R. Smith. July 6, 1897.
2	3	W. Manitoba, about 1700 ft., 5 miles W. of Virden.	Miss Mary G. Holmes. July 5, 1898.
1	1	Ontario, Lake Simcoe, De Grassi Point.	E. M. Walker. July 29, 1899.
1	—	Toronto, Golf Links, 5 miles E. of city.	E. B. Poulton. Sept. 23, 1897.
—	1	Toronto, Rose-dale.	E. B. Poulton. Aug. 25, 1897.
1 Aug. 19.	1 Aug. 27.	Northern Adirondacks, N.Y., Paul Smith's.	Rev. A. P. Hunt. 1903.
1 Aug. 17.	3 "Aug." Aug. 19 and 21	White Mountains, N.H., about 1800 ft., Colebrook, Parson's Farm.	Rev. A. P. Hunt. 1901.
5	2	Eastern States, probably Dublin, N.H.	Abbott H. Thayer. Probably Aug. 12, 1899.
3	5	Near Boston, Revere Beach.	Rev. A. P. Hunt. Aug. 2, 1901.
4 (including pair in cop.)	8	Chicago, waste land, S. of Jackson Park.	S. Watasé. W. M. Wheeler. E. B. Poulton. Aug. 5, 1897.
—	2	Chicago, E. of Lake Calumet.	W. M. Wheeler. E. B. Poulton. Aug. 6, 1897.
1	1	Kansas, Topeka, near Rock Island, R. R. Bridge.	C. L. Pribble. June 10, 1900.

it is easy to suppose that some of the original archippus with more orange than usual may have escaped capture on occasion from this cause. From such a small beginning, such as one may now see every year in *B. astyanax*, sprang doubtless the whole story, and we now find a butterfly which has for a ground color of both surfaces of the wings an orange which is the exact counterpart of that of *Anosia plexippus*; by reason of which in all probability it enjoys a freedom from molestation comparable to that attributed to *plexippus*, so that it ventures more into the open country than its allies, and thus gains a wider pasturage and surer subsistence" (l.c., p. 714).

The attempt will now be made to give an account of the changes in detail by which the mimetic pattern has been evolved from the entirely different pattern of the non-mimetic ancestor. The changes are somewhat more complex and probably more important upon the under surface which will therefore be considered first.

a. *Hind-wing Under Surface of Limenitis archippus*.—The black outer border to the white discal band of the hind wing of *arthemis* persists in *archippus*, but is much displaced inwards as compared with its ancestor. The reason of this is evident. The character in *arthemis* which initiated the mimicry of *Anosia* is the submarginal row of reddish spots, commonly found in the hind-wing, more rarely in the fore. The enlargement of these, as well as of the black-and-white-marked margin (also in mimicry of *Anosia*), has involved the shifting inwards of the black outer border of the white band. In many specimens of *archippus*, traces of the white band of *arthemis* may still be found for a greater or less distance along the inner edge of the black discal line. This vestige is especially often retained along the costal half of the line: it is occasionally well developed along its whole length. The original submarginal red spots are still recognizable between the discal line and the margin, being easily distinguishable by their deeper richer tint from the pale ground colour of the wing.

The black margin has become heavier, the double row of blue crescentic spots larger and whiter, but a faded trace of the original blue tint of *arthemis* can still be made out in the spots of the inner row, and remains distinct in the outer.

The basal red patches have vanished, but the pale blue



marks in and on the costal side of the base of the cell are retained, and, lightened in tint, represent the two more conspicuous white spots occupying nearly the same position in *Anosia*.

These changes, together with the transformation of a dark chocolate-brown ground-colour into a pale yellowish tint are the means by which the hind-wing under surface of the non-mimetic ancestral *arthemis* has become that of its beautifully-mimetic descendant, *archippus*.

b. *Fore-wing Under Surface of Limenitis archippus*.—The changes on the under surface of the fore-wing must now be considered. In *arthemis* the angulated black line, bordering the outer edge of the white discal band, runs from the costa to the anal angle of the wing. In *archippus* its anal extremity has been shifted upwards until it now joins the hind margin about at the junction of its middle and anal thirds. Rendered far more conspicuous against the ground-colour, greatly expanded at its costal end and there enclosing from two to four white spots, vestiges of the outer part of the white band, the marking now adds greatly to the mimetic resemblance, by its likeness to the subapical pale-spotted black band of *Anosia*. A further trace of the white band is generally seen on the costa itself, here often persisting for a distance equal to the normal width of the marking in *arthemis*. This character has also probably been retained because of its resemblance to the costal white markings of *Anosia*.

The two deep reddish patches in the cell of *arthemis* have disappeared in *archippus*, converted, with the ground-colour around them, into a fulvous tint considerably darker, as in the model, than that of the hind-wing and the apical region of the fore. Between these red patches in *arthemis* is a variable bluish triangular mark often pupilled with white and often surrounded by a black border. Other even more variable markings of the same kind are seen in the base of the cell. Although the red spots have disappeared in *archippus* the outer of these pale marks is, together with its black margin, almost always retained of full size but whiter than in *arthemis*. A trace of the basal mark or marks is also generally to be seen, sometimes only in the form of the black margin including a few pale bluish scales. This feature persists in a more complete state in the female specimens I have had the opportunity of examining. The outermost triangular pale mark, in spite

of its far more isolated position, probably represents a white spot, also triangular in shape, near the end of the cell in *Anosia*.

The marginal pattern is as in the hind-wing save that the apical white spots of the innermost series lose the crescentic shape and become squarish. The changes which have occurred in the subapical white spots of *arthemis* are peculiarly interesting. In *archippus*, only the costal spot and the second minute spot, generally a mere point, remain distinct and clear as in the ancestral form. The others—one to three in number—have become continuous with and contribute to form the triangular subapical pale yellowish patch which, in both mimic and model, is of the same tint as the ground-colour of the hind-wing. In the *Limenitis*, however, the outer (hind-marginal) part of this pale patch exhibits, as in the hind-wing, by a deeper tint, a distinct vestige of the reddish submarginal spots of *arthemis*. The single distinct costal white spot and minute second spot already referred to, appear to represent the extremity of a sickle-like curve within the apical angle of the fore-wing. All other parts of this curve are made up of the innermost series of marginal white spots—the ones which have undergone the principal increase in size in *archippus*. The effect is heightened by the special enlargement of the apical spot itself. Now when we turn to the model we find that the innermost series of marginal white spots does actually turn inwards sickle-like within the apex and that a close superficial resemblance has been attained in the mimic by the fusion of two separate elements. One of these has been preserved for the purpose out of an ancestral marking of which the remainder has been transformed in an entirely different direction.

The utilisation of the chief black and white markings of *arthemis* in the subapical region of the fore-wing of *archippus*, in order to promote the mimetic resemblance to *plexippus*, together with the value of the whitened marginal lunules of both wings is fully recognised by Scudder (l. c., p. 278).

c. *The Upper Surface of Limenitis archippus*.—The marginal band is much blacker and heavier looking than that of the under surface, in correspondence with the *Anosia* model. The markings in it consist only of the white sections of the fringe and the spots of the innermost series, the outer blue crescentic marks in the margin of *arthemis* having disappeared. The innermost crescents have become white and

in many individuals of *archippus* have lost their original form and gained a rounded shape. They often tend, as in the model, to be more strongly developed in the anal part of the series. Clear evidence of selection is seen in the relation between the degree of development of the black, white-marked marginal pattern in fore- and hind-wing of *arthemis* and *archippus* respectively. In *arthemis* this pattern is far more developed in the hind-wing than the fore, a condition reversed in *archippus* in accordance with the pattern of its model. A sickle-like curve is developed within the apex of the fore-wing in the same manner but not so fully as on the under surface.

The black outer border of the white discal band persists but is less heavy than on the under side. As on the latter surface it seriously interferes with the likeness to *Anosia* on the hind-wing, but enters into the mimetic pattern on the fore. Vestiges of the white discal band were not found on the upper surface of the hind-wing in any of the numerous specimens I have examined (although occurring in the form *hulsti*, Edw.); nor was the black band entirely wanting from any. A variety without this latter marking is however known and has been described as *pseudodorippus*, Strecker. The type of this form exists in Dr. W. J. Holland's collection ("Butterfly Book," New York, 1899, p. 185). On the fore-wing, vestiges of the white band persist and enter into the mimetic pattern, but they are far more reduced than on the under surface, in correspondence with the fact that many of the orange apical spots on the upper surface of the model are represented by white on its under surface.

The triangular pale spot in the cell of the fore-wing is usually represented on the upper surface by its black border only, but in a considerable proportion of individuals the white centre persists in a conspicuous form. In many individuals of the ancestral *arthemis* the same marking appears on the upper surface as a white point, generally very minute and often developed unequally on the two sides.

d. *The white spots on Body and Appendages of Limenitis archippus*.—There appears to be great variation in *arthemis* in the development of these pale spots and markings, but there is no doubt about their great increase in size and brilliancy in *archippus* and conversely their great reduction in *astyanax*. Pale spots corresponding to the brilliant white marks of *archippus* are always to be found in some

individuals of *arthemis*. This development in the mimic of course corresponds to the conspicuous body and leg pattern of the Danaine model.

LIMENITIS ARCHIPPUS, F. HULSTI, EDW., A BETTER MIMIC THAN ARCHIPPUS ITSELF.—In this Arizona and Utah form, as described and figured by Dr. W. J. Holland ("Butterfly Book," pp. 84, 185, Pl. VII, fig. 5), the black discal band on the hind-wing upper surface is evanescent, although distinct traces of the white band persist as a series of internervular spots. I have not had the opportunity of examining the under surface pattern. Dr. Holland states that the species occurs in Arizona with *Danaida berenice* and its form *strigosa*, Bates, and that it more closely resembles the latter. It is not unlikely that the vestiges of the white band on the hind-wings may, when the insect is on the wing, conduce towards a general likeness to the pale-streaked hind-wings of *strigosa*. Dr. Holland's figure indicates that, in the reduction of the subapical black of the fore-wing and the appearance of the associated white spots, *hulsti* has been modified from mimicry of the *Anosia* into resemblance to *Danaida*. Dr. Holland also draws attention to the dull tint of its ground colour as compared with *Limenitis archippus*, another change in the same direction.

LIMENITIS ARCHIPPUS, F. FLORIDENSIS, STRECKER (EROS, EDWARDS), A MIMIC OF DANAIDA BERENICE.

This example of mimicry is nearly as well known as that of *archippus* for *Anosia* (see e. g. Scudder, l. c., p. 718). At the same time, so far as I am aware no attempt has been made to compare the details of the resemblance in the two mimics in relation to the patterns of their respective models.

That *floridensis*, Streck., is a modification of *archippus*, under the influence of a second Danaine model (*berenice*), and is not the result of an independent evolution from *arthemis*, is at once evident from the persistence in it of features which are truly mimetic in *archippus* but tend to interfere with the resemblance to the existing Danaine model. Such features are seen on the upper surface, in the heavily blackened veins, and the large black triangular subapical markings on the fore-wing, as well as in the corresponding markings on the under surface. These features are, however, greatly obscured by the deepening of the ground colour into a dark mahogany-brown, like

that of the Danaine model. For the same reason the black margin is wider on both surfaces than in *archippus*. On the upper surface the white spots in the margin are much reduced and the white sections of the fringe slightly so, while on the under these markings remain conspicuous and distinct, much as in *archippus*. The sickle-like curve of white spots is seen at the apex of the fore-wing in *berenice*, and this feature is represented in *floridensis* in the same manner as in *archippus*. On the under surface the hind-wing of the Danaine is strongly veined so that the original mimetic feature of *archippus* holds good for the new model. This is not the case in the fore-wing where it detracts from the resemblance. The darkening of the ground colour of the under surface of *floridensis* is especially remarkable because here the more ancestral mimic had acquired so pale a tint, in mimicry of *Anosia* which has an under side far paler than its upper. In *berenice*, on the other hand, the tints of upper and under surface are approximately the same. Against this dark ground all the white markings stand out far more prominently in both model and mimic than in *Anosia* and *archippus*. The basal costal light mark of the fore-wing under surface is more uniformly distinct in the few specimens of *floridensis* I have seen than in those of *archippus*; and the white spots bordering the black discal line of the hind-wing under surface are also more developed and certainly more distinct, being in fact often given a clear outline by means of a black margin on their inner edges. Here we have evidently the emphasis and in a sense the re-call of a vanishing character in consequence of the conspicuous spots around the end of the cell in the hind-wing under side of the new model, *berenice*.

Scudder describes the form *floridensis* (*eros*) as ranging into the Mississippi valley and Dakota, far beyond the limits of its Danaine model. It would be very interesting to know the proportionate numbers of such specimens and to compare them with those from Florida, and ascertain whether the mimetic resemblance is in any way affected. Hitherto I have only had the opportunity of examining specimens from Florida.

In addition to the differences in pattern which distinguish *floridensis* from *archippus*, Dr. W. J. Holland states that the former is generally the larger (l. c., p. 186), and this is the case with the specimens I have studied.



## THE PAPILIONINE MODELS OF LIMENITIS ASTYANAX.

Before considering the evolution of *astyanax* from *arthemis* it is expedient to deal with the models, which in this case are Papilionine and not Danaine.

The late Erich Haase ("Researches on Mimicry," part ii, Stuttgart, 1896, English translation) discovered the wide extent of mimicry within the *Papilioninæ*, showing that the section to which he gave the name of *Pharmacophagus* tended to supply models for his two other sections of the *Papilioninæ*,—*Papilio* (of which *machaon*, L., may be taken as a type) and *Cosmodesmus* (of which *podalirius*, L., may be taken as a type). He showed that this is true of both areas inhabited by *Pharmacophagus*—the New World, and, in the Old, the Australian and Oriental Regions, and the parts of the Palearctic adjoining the latter. Outside these areas *Pharmacophagus* is only represented by the single species *antenor*, Drury, of Madagascar. Rothschild and Jordan in their recent exhaustive and admirable monograph on the American Papilios (Nov. Zool., xiii, 1906, p. 411–752) entirely confirm Haase's triple division of the *Papilioninæ* and show the numerous mistakes that have been made by systematists in inferring relationship from the superficial resemblances due to mimicry.

Haase failed, however, to appreciate the true nature of some of these mimetic associations because of his imperfect recognition of the scope of the Müllerian principle. He failed to do so in the case of the models of *astyanax*. As in other examples, Haase regarded the distasteful Central and North American "*Aristolochia* Swallowtail" (to use Rothschild and Jordan's term), *Pharmacophagus philenor*, L., as the central model round which were clustered species of his section "*Papilio*" as well as the Nymphalines, *Limenitis astyanax* and the female of *Argynnis* (*Semnopsyche*) *diana*, Cr.\*

But the resemblance of these two Nymphalines to the primary model *philenor* is so poor that the suggestion is

\* The mimetic resemblance of the dark southern ♀ form of *Papilio glaucus* (*turnus*) to *P. philenor* is also mentioned by A. R. Wallace ("Darwinism," London, 1889, p. 248) and Weismann ("The Evolution Theory," 1904, English translation, i, pp. 110, 111). Wallace also (l.c.) speaks of the likeness of *Limenitis ursula* (*astyanax*) to *philenor*.



unconvincing, and most naturalists will agree with Scudder in his hesitation in accepting it. At the same time, Scudder points out that the female *Argynnis* is an undoubted mimic of the *Limenitis*, but he, also failing to recognise the scope of the Müllerian principle, was only puzzled by the fact.

In the following pages it will be argued that *philenor* is the central primary model mimicked by both sexes of *Papilio troilus*, L., by the female and on the under surface by the male of *P. asterius*, Cr., and by the dark female form (*turnus*, L.) of *P. glaucus*, L., but that strong secondary resemblances exist between these three mimics, rendering them far more like each other than they are to the primary model; that the *Limenitis* is a secondary mimic of these three mimics, and the female *Argynnis* a tertiary mimic, perhaps a Batesian mimic, of the *Limenitis*.

#### THE GEOGRAPHICAL DISTRIBUTION OF PAPILIO (PHARMACOPHAGUS) PHILENOR AND ITS PRIMARY, SECONDARY AND TERTIARY MIMICS.

The distribution of the *Papilioninæ* is taken from Rothschild and Jordan's account, that of the *Nymphaliniæ* from Scudder's.

##### *Papilio philenor*, L.

Distribution. Mexico and the United States, except the central district from Colorado northwards; in Southern Canada and New England as a straggler.

In the subspecies *orsua*, Rothsch. and Jord., from the Tres Marias Islands, the tail of the hind-wing is represented by a tooth-like projection and the glossy area on the hind-wing upper surface is more extensive and more brilliant.

The larvæ of *philenor* are gregarious when young and semi-gregarious later in life (Scudder, p. 1248-9). The perfect insect is very tenacious of life, and Edwards states that it has a strong and disagreeable scent.

The three Papilionine mimics are placed by Rothschild and Jordan in three different groups of the section "*Papilio*," Haase ("Fluted Swallowtails," Rothsch. and Jord.).

## V. MACHAON GROUP.

60 c. *P. polyxenes asterius*, Cram.

South and north, from Honduras to Canada: west and east, from Arizona and the Mississippi basin to the Atlantic. Females mimetic throughout the range. Males mimetic on under surface, but non-mimetic on upper except the form *ampliata*, Ménétr., common at Guerrero, Mexico. Intermediates between *ampliata* and the males with non-mimetic upper surface are also common in the same locality.

60 a. *P. polyxenes americus*, Kollar, from N. Peru to Colombia and Venezuela, also has a dark form of both sexes, *melasina*, Rothsch. and Jord., with all inter-gradations between it and the light type form. The special mimetic features of the female *asterius* are not developed in this dark form, which is of great interest in helping us to understand the evolution of the northern mimic from a comparatively simple melanic variety.

The larva of *asterius* is said to resemble that of *Anosia plexippus* (Scudder, l. c., p. 747).

## VIA. GLAUCUS GROUP.

In Rothschild and Jordan's memoir two consecutive groups, of which this is the second, are both accidentally numbered VI. I have therefore called this VIA.

79 a. *P. glaucus glaucus*, L.

Atlantic district, from Florida to New England, and westward to Mississippi basin. The female form *glaucus* resembling the male is the ordinary one in the northern districts, while the mimetic form *turnus* is commoner than it in the southern. Intermediates occur but are rare.

79 b. *P. glaucus canadensis*, Rothsch. and Jord.

Newfoundland, Anticosti, New Brunswick, Canada to the north of British Columbia and Alaska. The females resemble the males, and mimetic forms are unknown in this subspecies, and the other species of the group.

## VII. TROILUS GROUP.

Allied to the highly mimetic ANCHISIADES GROUP, with gregarious larvæ.

Contains only two species, of which one is mimetic and the other probably non-mimetic, although incipient mimicry is possible on the under surface.

85 a. *P. troilus troilus*, L.

From Georgia to Canada: westward to Texas and the Mississippi plains: north-westward to N.W. territory of Canada.

85 b. *P. troilus texanus*, Ehrm.

Florida, in spite of the name. Probably a more primitive form in which the mimetic resemblance is less advanced than in 85 a.

86 a. *P. palamedes palamedes*, Drury.

Florida to Philadelphia, and westward to Mississippi plains.

86 b. *P. palamedes leontis*, Rothsch. and Jord.

A small form. Monterey, Mexico.

*Limenitis astyanax*.—The distribution is thus given by Scudder:—"It ranges from the Atlantic westward to the Mississippi Valley, and from the Gulf of Mexico northward to about the 43rd parallel of latitude." A closely allied species or more probably a form of the same species is recorded by Godman and Salvin from Mexico.

*Argynnis (Semnopsyche) diana*, Cr.—Scudder describes the distribution of this species as follows:—"An inhabitant of the hilly country of the south, following the Alleghanies, and a comparatively narrow belt westward at about the 38th parallel of latitude." How far westward it extends is unknown (p. 1801.)

The account given above shows that there is a very close coincidence between the distributional areas of the six species. When the area is comparatively restricted, as in the case of *A. diana*, it is still, as Scudder points out, altogether included within that of the species which its female most closely resembles, viz. *Limenitis astyanax*.

THE EVIDENCE THAT PAPILIO PHILENOR AND ITS MIMICS OCCUR AT THE SAME PLACE AND TIME. There is unfortunately at present far too little evidence on this subject. The small amount of material in the bionomic series of the Hope Department is tabulated below.

<i>Philenor.</i>	<i>Troilus.</i>	<i>Asterius.</i>	<i>Glaucus.</i>	LOCALITY.	CAPTOR AND DATE.
1 ♂ 58th Street, near the University.	1 ♀ 59th Street, near the University.	1 ♀ Jackson Park, the Island. July 28.	1 ♂ 59th Street, near Hotel del Prado.	Chicago.	E. B. Poulton, Aug. 10, 1897. Except <i>asterius</i> .
1 ♂ 58th Street, near Woodlawn Avenue.					
1 ♂ Aug. 1901.*	2 ♂ 1 ♀ Aug. 9. 1 ♂ Aug. 24.	1 ♀ Aug. 9.	—	Rutherford, N. J.	J. Cook. 1902.
3 ♂	—	1 ♂	—	Arizona, S. bound- ary of, Nogales.	R. C. L. Perkins. April, 1897.†

\* Probably a slip for 1902. The specimen has no original label upon it.

With regard to *Argynnis diana* I have no further information, but there is evidence that *L. astyanax* occurs with the Papilios. Thus Scudder states (p. 287) that it is persecuted by *Papilio asterius*. It is possible that, as in other cases which have been observed, the male *asterius* may pursue *astyanax* in mistake for its own female. Professor Bateson has informed me that he took *astyanax* with at least one of the above-named Papilios (probably *P. troilus*) and that he was greatly impressed with their resemblance in the field. In fact, if I understood him rightly, his general impression at the time was that he was observing a single species. Mr. J. C. Moulton has recently shown me six specimens of *astyanax* and one of the *turnus* female of *P. glaucus*, from a small collection of butterflies recently made at Sioux, Iowa, by Mr. C. H. Griffith.

THE RELATION OF THE TURNUS FEMALE OF PAPILIO GLAUCUS TO (1) THE PRIMARY MODEL, *P. PHILENOR*; (2) ITS CO-MIMICS IN THE PAPILIONINÆ.

At first sight the under surface of the dark southern mimetic female of *P. turnus* appears to be little more than that of a melanic variety in which the characteristic black markings of the fore-wing can be seen in deeper pigment than the ground colour. A remarkable feature is the persistence of a pale patch of ground colour just inside the end of the cell. In the non-mimetic females this very patch is more or less cut off by dark pigment from the rest of the pale ground colour, and it is an interesting fact that the isolated ground colour should remain pale while the rest has darkened. When the details of the mimetic resemblance are examined it is at once seen that the form *turnus* is far more than a mere melanic transformation of the female *glaucus*. There is a persistence of every element that aids in the superficial resemblance to the co-mimics and to the central model, *philenor*:—the marginal and submarginal series of yellow markings of the fore-wing, and the yellow marginal and deep orange submarginal series of the hind-wing, and between these two series the great intensification of bluish-green, margined internally with bright blue.

On the upper surface of *turnus* the adaptive nature of the transformation is even more evident. The blackness here is far more intense than on the under surface, and obliterates all the black markings of *glaucus*, any of which

would interfere with the mimetic resemblance to *philenor*. On the surface of the hind-wing the melanic transformation is accompanied by a great development of the iridescent blue scales, extending inwards into the cell, and also upwards to the costa and beyond into the neighbourhood of the anal angle of the fore-wing. In the few specimens I have had the opportunity of examining the colour of these scattered scales was bright blue and not bluish-green as in the submarginal region of the under surface. The yellow marginal and submarginal markings of the upper surface remain and contribute towards the resemblance to *philenor*, although the submarginal series is much nearer to the border of the wing than in the primary model. As regards the yellow colour, the *turnus* form is the least perfect of the three Papilionine mimics; for the submarginal spots of *troilus* (although yellow in the more ancestral non-mimetic *palamedes*) have gained a peculiar bluish-green colour in mimicry of *philenor*, while those of the female *asterius* have undergone a slight modification in the same direction.

In another very important element, however, the under surface of the *turnus* female is far nearer to *philenor* than are any of the other Papilionine mimics:—the existence of a single instead of a double row of bright orange-red submarginal spots on the hind-wing, although these are much closer to the margin of the wing than in the primary model. On the other hand, a second inner row of such spots is not present in the male or the ancestral female which resembles it. In the position of this inner row four wedge-shaped dull red marks are to be seen in the ancestral pattern, and the persistence of these, intensified by contrast with the dark ground colour, in the *turnus* form, is probably related to the presence of the inner row in *asterius* and *troilus*. They certainly interfere with the resemblance to *philenor*.

Each of the first four orange spots (counting from the costa) on the hind-wing under surface of *philenor* is edged with glistening white on the side towards the apical angle of the wing, the fifth is edged on both sides, the sixth towards the anal angle but not on the other side, while the seventh is not edged at all. In this respect the pattern of *turnus*, although by no means identical with *philenor*, approaches the latter more closely than do any of the other Papilionine mimics.



As regards the blue-edged green iridescence, the hind-wing under surface of *turnus* much resembles that of the female *asterius*. On the upper surface of the same wing the limitation of the submarginal blue iridescent scales by a black line (representing the inner boundary of the heavy black submarginal band of *glaucus*) also strongly suggests the female *asterius*, while the development of blue iridescence over the disc of the wing beyond this limit resembles *troilus*. The female of *asterius* is characterised by the absence of iridescence on the basal side of a black line corresponding to the limit above described. In place of the discal iridescence there usually appears on the hind-wing of the female *asterius* a more or less well-preserved vestige of the conspicuous yellow band of the male, extending, although in a less developed state, into the fore-wing. These features render the female *asterius* a less perfect mimic of *philenor* than are the other Papilios, although in the fore-wing of the male *troilus* a corresponding band is generally found, but in a far more vestigial condition. On the under side of the fore-wing in both sexes of this species as well as of the female *asterius*, this same band is far more evident, but undoubtedly concealed in the natural position of rest.

#### SECONDARY MIMETIC RESEMBLANCES BETWEEN THE THREE PAPILIONINE MIMICS OF P. PHILENOR.

The resemblance between these three mimics is stronger and more evident than might be inferred from the comparison of details contained in the last section. The dominant element in this secondary resemblance is the character of the blue and greenish tints on both surfaces. These in all the mimics present an appearance markedly different from that of the primary model, *philenor*, with its brilliant steely lustre. The remarkable likeness between the two rows of orange-red spots on the under side of the hind-wing in *asterius* and *troilus* is another important point, as also the fact that the female form *turnus* is prevented from being a mere melanic form of *glaucus* not only in details which resemble the primary model but in those which resemble its co-mimics. Upon the wing or even at rest from a little distance, all three mimetic Papilios would present the closest likeness to one another.

The larger of the two red spots near the anal angle of

the hind-wing upper surface in the *turnus* female is in nearly the same position as the one conspicuous spot of *asterius* and *troilus*, while at the apical angle of the same surface of the same wing, a large red spot appears in *turnus* and *troilus*. Red spots are not found in either position on the upper surface of *philenor*. These spots are certainly ancestral in the *turnus* female, inasmuch as they are present in the non-mimetic female form and the non-mimetic male of the same species, as well as in the allied non-mimetic species. For the same reason the black-pupilled red spot at the anal angle of *asterius* is ancestral. In *troilus*, on the other hand, both red spots are probably of recent origin on the upper surface, and have been developed in relation with the mimetic appearance. They are yellow in the ancestral *palamedes*. It is probable that their red colour in *troilus* has been developed in secondary mimicry of *asterius* and the *turnus* female form of *glaucus*. It is in accordance with this interpretation that the red spot at the anal angle of *troilus*, although without the black pupil, bears considerable superficial resemblance to that of *asterius*, and that the red spot at the apical angle is especially well developed in the female.

The comparison of these three mimetic forms also yields evidence of an approach towards the primary model, in which the different species have made different rates of progress, presumably determined in large part by the age of the mimetic resemblance.

*Papilio troilus* is evidently the oldest mimic. The mimetic likeness, extending to both sexes, has been derived from a very different appearance still preserved in *palamedes*. The suppression in *troilus* of the fifth orange-red spot of the inner row of *palamedes* is apparently an advance in the direction of the open loop of spots which is the prominent feature in the hind-wing under surface of *philenor*. Equally clear advance is seen in the bluish tint which the submarginal yellow spots of the upper surface of *palamedes* have gained in *troilus*.

*Papilio polyxenes asterius* is less perfect and presumably less old as a mimic than *troilus*. The mimetic resemblance is found on the under surface of both sexes, but on the upper the male, if a mimic at all, has only reached an early stage in the resemblance. The evolution of the two rows of definite orange-red spots out of the ill-defined elements found in the non-mimetic ancestors, was probably

effected under the influence of *troilus*. The ancestral yellow submarginal spots have darkened, but to a far less extent than in *troilus*.

Finally in the *turnus* form of the female *Papilio glaucus*, only found in a certain proportion of the females in the southern part of the range, we have the youngest of these mimics. The mimetic resemblance is in some respects less perfect than in the other two *Papilios*, but, as regards the red spots of the hind-wing under surface, it has been already shown that this form presents the closest likeness of the three.

THE EVOLUTION OF THE MIMETIC PATTERN OF LIMENITIS  
(BASILARCHIA) ASTYANAX FROM THAT OF THE NON-  
MIMETIC L. ARTHEMIS.

As regards the upper surface of *astyanax* the main and almost the only difference from *arthemis* consists in the disappearance of the white band of both wings, together with all but a trace of the subapical white markings of the fore-wing, and the spreading of an iridescent blue or greenish tint over and within the area formerly occupied by the band. Towards its inner limits the iridescent tint fades gradually into the dark ground colour of the wings. The iridescence is clearly an extension of the colouring seen in the marginal markings of *arthemis*. The dimorphism in tint—blue or greenish—is characteristic of the ancestral form no less than of its descendant. The reddish submarginal spots commonly seen on the hind wings of *arthemis* are rarer and far less developed in the specimens of *astyanax* which I have seen. The converse relationship holds in the fore-wings, where however the red spots are less developed in *astyanax* than in the hind-wing of *arthemis*.

Upon the under surface the changes are greater; for not only is there a similar disappearance in *astyanax* of the white markings of *arthemis*, but the whole ground colour has become of an iridescent dark greenish-brown, against which the reddish spots near the base of both wings and in their submarginal region, show up very prominently. Although from this cause far more conspicuous, the submarginal red spots of the hind-wing have become greatly reduced in *astyanax*, in correspondence with the increase in size of the crescentic black and

iridescent markings lying immediately external to them, and forming an elaborate marginal pattern. It is to be observed that in *artemis* itself the tint of the ground colour of the under surface and consequently the degree of prominence of the reddish spots varies very greatly, and that therefore an important element in the change from the ancestral to this mimetic form was pre-existent in the parent species and ready for selection to seize upon.

Passing to a very different relationship between the two species, the flight of *astyanax* is described as similar to that of *artemis*, but still more lofty and grand, more leisurely and sweeping. (Scudder, p. 287.)

#### L. ASTYANAX A SECONDARY MIMIC OF THE PAPILIO MIMICS OF PHILENOR.

Passing now to the mimetic relationships of *astyanax*, there can be no doubt that the iridescent blue or greenish of its upper surface resembles that of the Papilionine mimics rather than the primary *Pharmacophagus* model, although it approaches the brilliant steely lustre of the latter somewhat more closely than do the secondary mimics. Of all the three mimetic Papilios, *astyanax* chiefly resembles *troilus*, in which the submarginal crescentic spots are blue or greenish, instead of dull yellow as in the female *asterius*, or bright yellow as in the *turnus* female of *glaucus*. On the other hand, neglecting this feature, the blue varieties of *astyanax* would most closely resemble this latter form. These same blue iridescent examples of the *Limenitis* also resemble the females of *troilus*, in which the black ground colour is powdered with iridescent blue scales, forming a crescentic band inside the submarginal greenish spots. The greenish forms of *astyanax* similarly resemble the male *troilus* in which the iridescence is of a peculiar greenish-grey.

As regards the hind-wing under surface, the submarginal reddish spots of *astyanax* resemble those of the *turnus* female of *glaucus* less distantly than those of the other Papilios. But the resemblance to any of the three is in this respect only feeble. The basal reddish spots of *astyanax* may however, with the submarginal series, give something of the effect of the double row of the other two Papilios, or perhaps in the attitude of repose the basal and submarginal reddish spots of the *Limenitis* may be

to some extent joined up by those of the fore-wing under surface, forming a loop roughly suggestive of *philenor*.

Scudder regards *astyanax* as a very weak and perhaps incipient mimic of *Papilio* (*Laertias*) *philenor* (p. 287). Had the conception of secondary mimicry been before him, Scudder would have recognised that, although *astyanax* is, as he states, but a poor mimic of the primary model, *philenor*, it bears a considerable superficial likeness to the three Papilionine mimics of this species.

TRANSITION BETWEEN ARTHEMIS AND ASTYANAX.—The intermediate form *proserpina* is considered by Scudder (l. c., p. 289) to be a hybrid between *arthemis* and *astyanax*. In support of this conclusion he brings forward strong evidence based on distribution. *Proserpina* is found in a narrow belt across the eastern third of the continent, this belt coinciding with the southern boundary of *arthemis* and the northern of *astyanax*. Along this line it is known to occur at many points. *Proserpina* tends itself to vary in the direction of *arthemis* to the north and of *astyanax* to the south. The fact that Edwards bred *arthemis* and *proserpina* from the eggs of the latter is consistent with the view that the parent was a heterozygote (hybrid), whose offspring were yielding parent forms and heterozygotes, perhaps in Mendelian proportions.

In the collection of the British Museum *astyanax* and *proserpina* are regarded as forms or subspecies of *arthemis*, the form *lamina* of the latter supplying the connecting link.

TRANSITION BETWEEN ASTYANAX AND ARCHIPPUS.—Hybrids between these two forms are considered probable by Scudder (l. c., p. 283). Thus he quotes Meade (Can. Ent. iv, p. 217) "who found an *astyanax* on whose upper surface the blue was supplanted by fulvous 'except in the marginal lunules, which are white with a faint bluish tinge.'" He also refers to Grey (*Ibid.* xi, 17) for "a melanitic form of *disippus* [*archippus*] with all the markings of *ursula* [*astyanax*] on the under surface." Professor Bateson has kindly called my attention to further notes on such intermediates, with figures, in "Psyche" (1904, Feb., and 1907, Oct.).

It is therefore probable that occasional interbreeding takes place between *astyanax* and *archippus*, and that



hybrid offspring are produced. If this be so it would constitute further evidence of the close affinity between these three forms, and of the recent operations of the selective processes by which the two mimics have been derived from their non-mimetic ancestor.

ARGYNNIS (SEMNOPSYCHE) DIANA (FEMALE) A TERTIARY MIMIC OF LIMENITIS ASTYANAX.—This interesting case of mimicry was, so far as I am aware, first suggested by Scudder, who was much puzzled by it. This distinguished authority remarks concerning *diana* that although it belongs to a group remarkable for resemblance between the sexes, its sexes are more strongly contrasted than those of perhaps any other butterfly in North America. "This difference, as we have pointed out in the body of this work, is a clear case of parastatic mimicry, the mimicry affecting the female only (as most in need of such protection), and is the more surprising since the butterfly mimicked belongs to the only genus in our fauna, where, in other species, parastatic mimicry of a Euploeid butterfly occurs. If a butterfly of the genus *Basilarchia* needs protection and gains it by mimicry of *Anosia* or *Tasitia*, why should *Semnopsyche* take to imitating a normal *Basilarchia*? That it does closely resemble it any one can see, and the following passage from Edwards, writing of the discovery of the female, may be taken in evidence: 'While breaking my way through a dense thicket of [iron-weed], hoping to find another *diana* [male], I came suddenly upon a large black and blue butterfly, feeding so quietly as to allow me to stand near it some seconds and watch its motions. It seemed to be a new species of *Limenitis* [*Basilarchia*], allied to *ursula* [*astyanax*], which it resembled in color.' It may also be pointed out that its range is altogether included within that of *Basilarchia astyanax*" (l. c., p. 1802). Although the obvious interpretation of this interesting resemblance on the probable hypothesis that *Limenitis* (*Basilarchia*) is a distasteful genus and its mimicry of *Anosia* Müllerian, seems to have escaped Scudder in this passage and on p. 718, he elsewhere suggests (on p. 266) that *astyanax* may be specially protected:—"It is indeed possible that one of the normally colored species of *Basilarchia*, one that has least conspicuously contrasted colors, though resplendent with blue and green, is specially protected by the various



other devices we have recounted; for certainly it is itself mimicked by one sex of a butterfly of another very distinct group, viz. *Semnopsyche diana*."

The female of *A. diana* is only mimetic of *astyanax* on the upper surface. There is, however, far less sheen about the blue tint of *diana*, and in this respect it approaches the *Papilio* mimics of *philenor* more closely than it does *astyanax*, while the *Argynnis* is itself further removed from the primary model than any of the other mimics. Scudder speaks of the uniformity between the sexes of the group to which *diana* belongs; but Dr. F. A. Dixey has shown (Trans. Ent. Soc. Lond., 1890, pp. 89-129) that the females of *Argynnis* often tend to be dark, and he points to *A. paphia* as a well-known example of a species with a dark female form,—*valexina*. He gives strong reasons for the belief that such dark forms are ancestral, and that among them the female of *diana* is especially primitive.

It is a probable hypothesis that the recent evolution of *L. astyanax* provided this ancestral form with a model which it could approach by small and easy steps of variation. In this way it is possible to explain the appearance of the only character which, in Dr. Dixey's opinion, "is really peculiar to *A. diana* among its relatives . . . [viz.] the large expanse of blue ground colour . . ." which Dr. Dixey admits to be "like the corresponding feature in *B. astyanax* and *L. philenor*" (l. c., p. 106, footnote).

## LIMENITIS (ADELPHA) CALIFORNICA, THE NYMPHALINE MODEL OF LIMENITIS LORQUINI.

The dominant genus *Adelpha* is the close ally and tropical American representative of the Holarctic and Oriental *Limnitis* (s. l.). *Chlorippe*, as employed by Godman and Salvin, is similarly the Neotropical representative and near ally of *Apatura*. The females of certain Palæarctic *Apaturas* such as our own *A. iris*, L., are probably rough mimics upon the upper surface of the black white-marked species of *Limnitis*, such as *L. sibylla*, L. I have found in the Sierra Guadarrama, Spain, *Apatura iris*, L., flying with *L. camilla*, Wien. Verz., and closely resembling it upon the wing. The males of these species with their beautiful

blue iridescence are far less perfect mimics. Similarly in the Neotropical Region many species of *Chlorippe* have brilliantly iridescent blue males, while the females are beautifully mimetic of *Adelphas*. In other species both sexes are mimetic of the same genus. These *Chlorippes* differ from the *Apaturas* in the much greater brilliancy of the males and the far closer mimicry in the females. Nor are they altogether restricted to the *Adelpha* models; for the female of *C. zunilda*, Godt., is a mimic of such a *Callicore* as *candrena*, Godt. As in *Apatura*, the mimetic resemblance of *Chlorippe* is confined to the upper surface.

The powerful genus *Adelpha*, with over 70 species, of which 31 extend into Central America, forms a homogeneous tropical group, at once distinguished by the hairiness of the eyes in front from the allied *Limenitis* of the northern belt. A single species with smooth eyes, provisionally included in the genus by Godman and Salvin, is not only removed from the other *Adelphas* by this feature, but also by its distribution; for its northern form, *A. californica*, Butl., ranges through California into Oregon, while the southern form, *bredowi*, Hübn., extending from Guatemala through Mexico into Arizona, reaches much further north than any other species of the genus. In the brief statements printed in the Proceedings of this Society (1907, pp. lxxvii, lxxix, lxxx) I have followed Godman and Salvin in provisionally retaining this remarkable form in the genus *Adelpha*, a position also assigned to it by Dr. W. J. Holland ("Butterfly Book," p. 187). Since these brief notes were prepared, Mr. G. A. K. Marshall has also studied its position, and I agree with him that *bredowi* and *californica* should be removed from the southern genus *Adelpha* and provisionally placed in the heterogeneous northern group, *Limenitis*, a position assigned to them by Scudder in 1875 (Bull. Buffalo Soc. N. Sc., Feb. 1875, p. 233). The hairy eyes appear to be the only consistent point of discrimination between *Adelpha* and the northern *Limenitis*, and even this distinction breaks down in the hairy-eyed Indian species of the latter group. The smooth eyes and the northern range support the removal of *bredowi* from *Adelpha*, while its very different male secondary organs are not alone sufficient ground for generic separation from *Limenitis* (*Najas*) *lorquini*. The evolutionary point of view also supports the removal of *bredowi* and *californica* from *Adelpha*. Omitting these

two outlying forms, the whole genus is evidently the outcome of prolonged isolation and specific differentiation in the Neotropical Region ; while there are no reasons, except those founded on superficial resemblances of colour and pattern for supposing that *californica* and *bredowi* are the outcome of any such history. But in removing these two forms from *Adelpha* and transferring them to *Limenitis*, they lose a place in a definite and probably permanent genus and enter a heterogeneous and obviously provisional assemblage. Already the majority of the North American species have been split off as *Basilarchia*, while *lorquini*,\* Boisd., has been included, with the European *populi*, in *Najas*, and the Chinese *albomaculata* separated as *Hypolimnethes*. All these changes fall far short of what is required, viz. a careful revision of the whole assemblage of species included under the old *Limenitis*. Until this task is undertaken the creation of new isolated genera or subgenera may obscure rather than reveal the true relationships, and I therefore prefer to follow Godman and Salvin in provisionally placing the whole of the species under *Limenitis* in the broad sense, at the same time directing attention with these authorities to the composite nature of the group and the necessity for its thorough revision. I only differ from them by acting upon the doubt which they express, and removing a discordant element from *Adelpha*.

The southern form, *Limenitis bredowi*, Hübn., occurs in Guatemala, Mexico and Arizona, the northern form, *L. californica*, Butl., in California and Oregon. An example from each of these localities is figured on Plate XXV. *Californica* is also recorded by Dr. W. J. Holland (l. c., p. 188) from Nevada, and it would be extremely interesting to ascertain whether, on the S.E. borders of this State and of California, it interbreeds with and is transitional into *bredowi*, in Arizona. Dr. Holland says of the northern form—"In its habits and manner of flight it closely resembles the species of the genus *Basilarchia*" (l. c., pp. 187-8). And of the larval stage the same authority writes (p. 187) :—"while in general resembling the caterpillars of the genus *Basilarchia*, the segments are adorned

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\* *Lorquini* was included, with the other N. American species, in *Basilarchia*, in Proc. Ent. Soc. Lond., 1907, pp. lxxvii, lxxix and lxxx, following the arrangement of Dr. W. J. Holland. By a printer's error which unfortunately escaped notice, "W" (for West) has been printed instead of N (for North) on p. lxxx.

with more branching spines and with short fleshy tubercles giving rise to small clusters of hairs."

THE SOUTHERN LIMENITIS (ADELPHA) BREDOWI A MIMIC OF THE NEOTROPICAL ADELPHAS.—Mr. Marshall has kindly compared the patterns of the extremely fine series of *Adelphas* in the British Museum with that of *L. bredowi*, and he finds that the latter most closely resembles, on both surfaces, *A. dyonyssa*, Hew., while, as regards the upper side alone, *massilia*, Feld., *lerna*, Hew., and *fessonia*, Hew., would come into the same assemblage. The yellowish tint of the band of *bredowi*, so clearly mimicked by *lorquini*, is apparently not itself a result of mimetic resemblance to the *Adelphas*; for all the Central American species have the band pure white or bluish-white, with the exception of *A. pione*, Godm. and Salv., and one or two species like it—all very dissimilar from *bredowi*.

#### THE GEOGRAPHICAL DISTRIBUTION OF THE WESTERN SPECIES OF LIMENITIS IN N. AMERICA.

*L. californica* occurs, as has been already mentioned, in Oregon, California and Nevada, and the southern *L. bredowi* in Arizona, Mexico and Guatemala; *L. lorquini* occurs with *californica* in the three first-named States, but extends much further north along the Pacific coast into British Columbia and Vancouver's Island. *L. weidemeyeri*, Edw., is described as ranging from the Pacific slope eastward to Montana, Nebraska and New Mexico. The 18 specimens in the British Museum are from Colorado and Utah. Scudder gives the distribution as the Rocky Mountain Region from Montana to Colorado (Bull. Buffalo Soc. N. Sc., Feb. 1875, p. 233) and concludes from the dates of specimens captured on the Yellowstone Expedition in 1873 that its periods resemble those of *B. arthemis* (Proc. Bost. N. H. Soc., vol. xvii, 1874-5, Ent. notes, IV).

The early stages of *weidemeyeri*, according to Edwards, resemble those of *L. archippus* (Can. Ent., xxiv, p. 107). The larvæ of *lorquini* are described by Dr. G. Harrison Dyar (l. c., xxiii, p. 172).

#### RELATION BETWEEN THE PATTERN OF *L. LORQUINI* AND THAT OF THE NON-MIMETIC *L. WEIDEMEYERI*.

In the above title I have not committed myself to the view that the pattern of *lorquini* has been evolved from

that of *weidemeyeri* in the manner that *archippus* and *astyanax* have sprung from *arthemis*. It is by no means improbable that, apart from the modifications which have produced a superficial resemblance to *californica*, the pattern of *lorquini* is more ancestral than that of the non-mimetic *weidemeyeri*.

On the upper surface the pattern of *lorquini* closely corresponds with that of *weidemeyeri*, but differs in the details described in the following section.

The apical area of the fore-wing is bright fulvous: the pale markings are cream-coloured instead of white: the whole discal band is placed nearer to the base of the wings, especially in the case of the hind: this band is also drawn out to a more pointed extremity towards the anal angle of the hind-wing: the constituent spots of the band, especially in the fore-wing, are more completely separated by strongly blackened veins.

An interesting feature possessed by certain individuals of both species is seen in the series of deep reddish spots, inconspicuous against the dark ground colour, placed along the outer border of the pale band in the hind-wing. These spots evidently represent the more prominent series commonly developed in *arthemis*. The complete series is occasionally quite distinct in *lorquini*; but as a rule the only conspicuous member is the spot at the anal angle of the hind-wing, where also a single spot of an outer series is often present. Of *weidemeyeri* I have had little material for careful study; but the red spots are faintly visible in one out of two specimens.

The inner edge of the white band of the fore-wing of *weidemeyeri* cuts the inner margin about opposite the centre of the white costal spot of the hind-wing, a spot much produced inwards towards the base of the wing as compared with the rest of the hind-wing series, as may be seen in Plate XXV, fig. 10 (in Fig. 1 the inward extension of the spot is concealed, especially on the left side, by the overlap of the fore-wing). In *lorquini*, which preserves the same general arrangement, the inner edge of the fore-wing band meets the costal spot of the hind-wing near its outer edge, thus forming a more pronounced step-like break than in *weidemeyeri*. The females of *lorquini* which I have had the opportunity of studying are in this respect in the condition of *weidemeyeri*. The white spot, which is almost invariably well developed in the fore-wing



cell of *lorquini*, is generally minute or altogether wanting in *weidemeyeri*. It is developed in the British Museum series of the latter species as follows:—Large on the upper surface in 1 male, of medium size in 1, minute in 7, and absent in 5 : of medium size in 2 females, very minute in 1, absent in 3.

Nearly the whole of the above points of distinction between the upper surface patterns of *weidemeyeri* and *lorquini* can be verified by the comparison of Figs. 1 and 10 with 6, 7, and 8, on Plate XXV. The example of *weidemeyeri* represented in Fig. 1 possesses an unusually well-developed spot in the fore-wing cell, while Fig. 10 represents an individual in which it is minute, especially so upon the left side. The relatively high development of this spot in *lorquini* is almost certainly ancestral, as is the subapical series of white spots in the fore-wing (less developed than in *weidemeyeri*); for both interfere with the mimetic resemblance to *californica* (compare Figs. 2 and 3 on the same Plate). The submarginal white spots, especially developed in the apical section of the fore-wing hind margin of *weidemeyeri*, have almost disappeared in *lorquini*. Faint traces can however generally be detected, as in Figs. 6, 7 and 8.

The difference in tint between the white band of *weidemeyeri* and the cream band of *lorquini*, *californica* and *bredowi* could not be shown by photography without detriment to other parts of the negative. Mr. A. Robinson, of the Oxford University Museum, got over the difficulty by colouring the parts which should have been cream with a wash of very dilute aniline colour in water. Plate XXV has been prepared from a print thus treated.

The under surface of *lorquini* differs from *weidemeyeri* in the strong development of a dark rich mahogany-brown, replacing more or less completely the bluish-grey tint of the basal half of the hind-wing and of the submarginal markings. So far as my experience goes this replacement is on the average carried much further in the examples of *lorquini* from Vancouver's Island.

In those individuals of *lorquini* in which the suppression of these pale markings is least pronounced, the inner row of submarginal lunules—bluish-grey in the hind-wing, white in the fore—is larger and more conspicuous than in *weidemeyeri*.



MIMETIC RESEMBLANCE STRONGER IN THE SOUTHERN  
EXAMPLES OF *LORQUINI* WHICH ARE GEOGRAPHICALLY  
COINCIDENT WITH CALIFORNICA.

The following features, described in the preceding section, promote a superficial resemblance of *lorquini* to *californica* :—

- (1) The fulvous apical area of the fore-wing.
- (2) The cream tint of the discal band crossing both wings.
- (3) The fulvous marking at the anal angle of the hind-wing.

Of these features the last is so excessively variable and so often absent in both northern and southern examples, that very long series would be required in order to compare the average development in the two areas. This element in the mimetic resemblance is apparently incipient and imperfectly established.

The discal band is apparently paler in the northern *lorquini* than the southern. The difference, which is excessively slight, may be best seen when a series of individuals are compared; but I do not think that the conclusion can be regarded as safely established until a large number of fresh specimens have been carefully examined from this point of view.

As regards the most important feature in the mimetic resemblance—the fulvous apical area—there is undoubtedly a much greater average development in the examples of *lorquini* from California and Oregon (Figs. 7 and 8 respectively) than in those from British Columbia and Vancouver's Island (Fig. 6), entirely beyond the range of the model.

In many of the southern specimens of *lorquini* the fulvous apical patch extends inwards (as in Fig. 8 on Plate XXV) nearly as far as the outer border of the costal end of the discal band in the fore-wing. The colour is of a richer deeper shade than the bright tawny patch of *californica*.

On the under surface the development of the inner row of submarginal bluish-grey lunules into a festooned band in a large proportion of the examples of *lorquini* is probably caused by mimetic approach to *californica*. At any rate the marking is often a more conspicuous feature

in *lorquini* than in *weidemeyeri*. The study of its relative development in the southern part of the range would require a much larger number of specimens than I have as yet had the opportunity of seeing. There is however no doubt that the feature is generally suppressed in Vancouver's Island and that it is usually well developed in British Columbia.

The undoubted affinity between *californica* and *lorquini* may lead naturalists to conclude that their resemblance is due to relationship and not to mimetic approach. It is commonly forgotten that mimicry, being *independent* of affinity, occurs between forms of all degrees of relationship, the closest as well as the most remote. When the chief mimetic element in the pattern of *lorquini* is examined it is at once apparent that the likeness is superficial, and that the appearance is produced in a manner entirely different from that of the model. The orange patch on the fore-wing of *californica* is a clearly defined sub-apical and submarginal marking, roughly resembled in the mimic, *lorquini*, by the inward growth of a brown marginal marking (compare Figs. 2 and 3 with 6, 7 and 8 on Plate XXV). There can be little doubt also that the cream tint of *lorquini* is not ancestral, but due to recent modification of white markings like those of *weidemeyeri*, *arthemis* and many Palæarctic species of *Limenitis*. The average increase of mimetic likeness in the area occupied by the model confirms in the most convincing manner the conclusion that the resemblance is due to mimicry and not to affinity.

DIFFERENCES BETWEEN CALIFORNICA AND BREDOWI ARE  
SUCH AS TO PROMOTE A RESEMBLANCE BETWEEN THE  
NORTHERN FORM AND LORQUINI.

- a. *The shape of the wings*.—The marked difference in the shape of the wings between the males of the northern *californica* and the southern *bredowi* is well seen by comparing Figs. 2 and 3 with 4, 5, and 9 on Plate XXV. This distinction, apparently, does not hold in the other sex; for the few southern females I have seen exhibited the proportions of the northern form. The difference was clearly explained, although without reference to the females, by A. G. Butler in his original description of *californica* (Proc. Zool. Soc. Lond., 1865, p. 486):—"the wings

are much more rounded than those of *H. Bredowii*, and are not produced at the end of the second median nervule." The more rounded shape of the hind-wings is also very clear in the northern form, those of the southern (Figs. 4, 5 and 9) being more triangular in shape, and the hind margin tending to form a straight line with that of the fore-wing to a greater extent than in *californica* (Figs. 2 and 3). In all these points by which the shape of *californica* is rendered different from that of *bredowi*, there is resemblance between it and *lorquini*.

b. *The fulvous mark at the anal angle of the hind-wings.*—It is unnecessary to describe this distinction in any detail; for the characteristic form of the marking is well shown in Figs. 4, 5 and 9, together with its diminution in the northern form (Figs. 2 and 3). It is barely seen in Fig. 3, although visible in the specimen itself. Fig. 2 however shows the marking distinctly and affords a fair comparison with the condition represented in the southern examples (Figs. 4, 5 and 9). Here too the divergence from the southern *bredowi* is coincident with resemblance between the northern form and *lorquini*.

c. *The step-like break in the band at the junction of fore- and hind-wings.*—As regards this feature *californica* is certainly far nearer than the southern *bredowi* to the appearance presented by *lorquini*. *Bredowi* approaches the condition, seen in many *Adelphas*, of a straight continuous band sweeping from fore-wing on to hind. Compare the representation of the southern form in Figs. 5 and 9, with those of the northern in Figs. 2 and 3, and the latter with *lorquini*, shown in Figs. 6, 7 and 8. The break on the inner margin of the band in the Arizona example represented in Fig. 4 is intermediate between the more northern *californica* and more southern *bredowi*. The difference between the right and left sides of Fig. 9 was probably caused by the "setting." The step-like break of *californica* is produced by the small size of the last pale spot on the inner margin of the fore-wing, as well as by the direction of the last spot but one, which is so placed that its inner border forms a considerable angle with that of the hind-wing band. If Figs. 4, 5 and 9 be compared in this respect with 2 and 3 it will be seen that the last spot of the southern form is much larger,\* while

\* This point of distinction between *californica* and *bredowi* was described by A. G. Butler in Proc. Zool. Soc. Lond., 1865, p. 465.

the last spot but one is twisted into a much closer coincidence with the inner border of the hind-wing band. As regards the position of the last spot but one, *lorquini* goes much further than *californica*, the direction of the inner border of the fore-wing spot coinciding with the outer border of the hind-wing band (Figs. 6-8).

Apart from the orientation of the last spot but one in the band of the fore-wing, the very characteristic hour-glass-like form seen in greater or less perfection in all the figures on Plate XXV is probably an ancestral feature. There appears to be no doubt that the indentation of the inner side of the spot tends to be obliterated and replaced by a straight contour in *bredowi* (compare Figs. 2 and 3 with 4, 5 and 9). In this respect the northern form is probably ancestral. At any rate an approach to *lorquini* in this feature is unlikely; for in *lorquini* itself the inner contour is less indented than in *californica*.

The fact that the break in *californica* approaches but does not equal that of *lorquini*, attaining in fact about the condition of *weidemeyeri* (see Figs. 1 and 10), supports the conclusion that in this respect *lorquini* acts as a model and *californica* as a mimic.

The step-like break, together with the more outward position of the spot below the end of the cell in *californica*, tends to give the band of the fore-wing an irregular zigzag W-like appearance, suggesting the form which is more fully and symmetrically attained in *lorquini*. The example of *bredowi*, represented in Fig. 9, is in the opposite condition, with a comparatively straight fore-wing band, while the specimens seen in Figs 4 and 5 are intermediate. The outward displacement of the spot below the cell of *californica* promotes this superficial resemblance to *lorquini*, in spite of the fact that the corresponding spot of the latter occupies a more inward position. It produces this effect by increasing the angulation of the irregular zigzag formed by the fore-wing band.

d. *The external border of the hind-wing band.*—The fifth spot (from the costa) of the hind-wing band of *californica* projects beyond the rest of the outer border to a greater extent than in *bredowi*, and thus disturbs the regular straight or slightly concave sweep which is so characteristic in the southern form. Although resembling no particular feature of *lorquini*, the difference probably promotes a general superficial resemblance to the distinctly convex

contour of the more interrupted hind-wing band of this species.

SLIGHTLY INCREASED RESEMBLANCE TO THE *ADELPHA* PATTERN IN THE MOST SOUTHERN EXAMPLES OF *BREDOWI*.

In one respect the upper surface of the most southern specimens of *bredowi*, from Guatemala, appears to show the influence of *Adelpha* more strongly than the more northern examples from Mexico and Arizona. In both the southern examples I have had the opportunity of studying there is a small fourth spot in the fore-wing band (counting from the costa), absent from the numerous more northern specimens of *bredowi* and *californica* which I have seen. This small spot is clearly shown, especially on the right side, in Plate XXV, fig. 5. It is considerably larger in a second Guatemalan specimen in the Hope Department. This feature tends to make the fore-wing band more continuous than in the specimens from further north. This spot is however generally represented on the under surface of *bredowi* from more northern parts of its range, and is often seen in the same position in *californica*.

HAS RECIPROCAL (DIAPOSEMATIC) MIMICRY BEEN ESTABLISHED BETWEEN *CALIFORNICA* AND *LORQUINI*?

There is only one apparent means of escape from the conclusion that we are confronted with a striking example of Diaposematic resemblance between those two species. It may be held that *californica* possesses an ancestral pattern from which *bredowi* in the south has been modified by mimicry of the prevalent *Adelphas*. In certain respects this interpretation is probably correct. Thus the form of the wings in the female of the southern subspecies supports the conclusion that their similar form in both sexes of the northern subspecies is ancestral. But it would, I think, be a curious coincidence if all the details by which the northern *californica* differs from *bredowi* and superficially resembles another species, should be ancestral survivals unconnected with the presence of that other species—*lorquini*.

Are we to regard the evident *Adelpha*-like elements in the pattern of *californica*—only less strongly marked than those of *bredowi*—as ancestral or as the result of mimetic influence spreading with diminishing effect beyond the



range of the models? The latter seems to be a far more probable hypothesis; for we have a good parallel example in *lorquini* itself, where the mimetic influence has been shown to lessen as the mimic passes northwards out of the range of its model. At the same time it must be remembered that species of *Limenitis* (s.l.) with an *Adelpha*-like pattern exist in the Oriental Region; and it is a possible hypothesis that these species and *californica* represent the ancestor of the Neotropical *Adelphas*. The cream-colour of the band of *californica* is at any rate an ancestral feature, unconnected with mimicry of the *Adelphas*.

We may hope with some confidence that this fascinating but difficult problem may receive a final solution when the structural relationships of all the species of *Limenitis* and *Adelpha* in their broadest sense shall have been made out in detail. In the meantime, as I have said above, the origin of nearly the whole upper surface pattern of *californica* as the result of the spreading northward of an influence exerted by the genus *Adelpha* in the south, appears to be the safest provisional conclusion to adopt. The following facts seem to support it and at the same time to suggest that reciprocal mimicry of *lorquini* has also taken place.

The number of species of *Limenitis* in N. America points to an ancient existence in this portion of the Holarctic Belt. At the same time their mimetic relationships in the eastern section of the Continent have been shown to be extremely recent. The change in *lorquini* as it passes north of the range of its model (*californica*), suggests that its mimicry is also extremely recent. That the North American *Limenitis* are highly susceptible to mimetic influence is shown in the fact that they contribute such a high proportion of the butterfly mimics of the Continent, and that they furthermore produce the most divergent mimetic patterns. In the eastern section of the Continent this recent development of mimicry has been shown to correspond to a recent invasion of Danaine models and to the influence of *Papilio*s—themselves mimics of recent date—exhibiting most beautiful examples of transition in the stages of developing mimicry. It is therefore extremely probable that the very recent mimetic pattern of *lorquini*—far more imperfect than that of any other mimicking *Limenitis* in America—also corresponds to the

recent appearance of an *Adelpha*-like model in a portion of its range. It is extremely difficult to believe that so imperfect a result would have been produced in a member of such a sensitive group if contact with the model had been prolonged.

Finally there is the fact that, as shown by Godman and Salvin, the southern form *bredowi* extends into Arizona much beyond the range of any true *Adelpha*, while examples from the most southern part of its range in Guatemala only exhibit, in the minute detail described on p. 485, an increased likeness to the *Adelphas*. The mimetic resemblance of *bredowi* is an established and stable product, but slightly increased by deepest penetration into the area of the models, maintained well beyond their northward limit, and only modified when the range of *lorquini* is entered in California.

The relationship of this interesting species to its *Adelpha* models indicates a marked susceptibility to influences of the kind, and supports the conclusion that the northern form has been reciprocally modified by the presence of its abundant mimic, *lorquini*.

## CONCLUSIONS.

### A. THE EASTERN SECTION OF NORTH AMERICA.

1. The Old World ancestor of the Danaine butterfly, *Anosia plexippus*, invaded the New World by way of the north, at a time sufficiently remote to permit of the acquisition of generic distinction.

2. The invader was mimicked by an indigenous species of *Limenitis*, closely similar to and probably identical with *L. arthemis*, which thus originated *L. archippus*.

3. A second closely allied Old World Danaine invaded the New World as *Danaida berenice*. This later invasion is so recent that the generic characters remain unchanged.

4. In Florida, the second Danaine intruder has modified the mimic of the earlier intruder into a superficial likeness to itself, thus producing the *floridensis* form of *L. archippus*.

5. The specially protected *Papilio* (*Pharmacophagus*) *philenor* is mimicked by three species of *Papilio*, the different stages to which the resemblance is carried indicating recent modification.

6. The three mimicking species of *Papilio*—*troilus*, *asterius* (female), and *glaucus* (female f.)—exhibit secondary mimicry of one another.

7. Secondary mimicry of these three *Papilios* has led to the evolution of *Limenitis astyanax* from *L. arthemis* at so recent a date that the two forms occasionally interbreed where they meet.

8. The female of *Argynnis diana* has been modified into a tertiary mimic of *L. astyanax*.

## B. THE WESTERN SECTION OF NORTH AMERICA.

9. An ancestral northern Nymphaline butterfly belonging to the heterogeneous group "*Limenitis*" penetrated the area of the dominant Neotropical genus *Adelpha* and gained a superficial resemblance to its much-mimicked pattern.

10. The influence of *Adelpha* spread far beyond the range of the models into the northern subspecies *californica*, which in turn influenced, and has probably itself been reciprocally influenced by, *L. lorquini*, in California and Oregon.

11. The influence of *californica* upon *lorquini* spreads northward, with diminishing effect, beyond the range of the model, into British Columbia and Vancouver's Island.

12. Some of the ancestral features of *lorquini* are preserved in the non-mimetic species *weidemeyeri*.

NOTE.—A further study of the larvæ of *Danainæ* tends to throw doubt upon the validity of *Anosia* as a distinct genus. Two pairs of filaments are borne by the larva of *plexippus* and of *genutia*, probably its nearest ally in the Old World: three pairs are similarly characteristic of *berenice* and its probable representative, *chrysippus*.

Dr. Jordan, who has examined the male genitalia, kindly informs me that *chrysippus* and *berenice* are of the same type, while *genutia* and *plexippus* are of a second type. He agrees that *plexippus* cannot be generically separated from the other brown *Danainæ*. E. B. Poulton, Dec. 16, 1908.

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## EXPLANATION OF PLATE XXV.

[See *Explanation facing the PLATE.*]